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Influence of Thermal Challenge on Conditioned Feeding Forays of Juvenile Rainbow Trout

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16. ABSTRACT

Juvenile rainbow trout (Salmo gairdneri) conditioned to traverse a 2.4-m-long channel to receive a food reward where subjected to in-transit thermal challenges. Conditioning was to a criterion that required 80% of the fish to leave the "home" area and reach the "reward" area within 2 minutes of release. Challenges were at successive 3 C increments above acclimation or the previous challenge temperature. Fish were first observed to delay their entrance into the intervening heated water at challenge temperatures of 12-15 C above acclimation. At each increment above 12-15 C over acclimation temperature, delay in transit increased; however, complete group inhibition was never achieved. Above their critical thermal maximum (CTM) the reward was achieved even at the expense of deaths among the achievers. Responses were the same whether fish were challenged individually or as groups. Fish exposed to their CTM without prior challenges at less stressful temperatures responded similarly to those receiving progressively greater challenges.

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Influence of Thermal Challenge on Conditioned Feeding Forays of Juvenile Rainbow Trout

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Abstract

Juvenile rainbow trout (*Salmo gairdneri*) conditioned to traverse a 2.4-m-long channel to receive a food reward were subjected to in-transit thermal challenges. Conditioning was to a criterion that required 80% of the fish to leave the "home" area and reach the "reward" area within 2 minutes of release. Challenges were at successive 3 C increments above acclimation or the previous challenge temperature. Fish were first observed to delay their entrance into the intervening heated water at challenge temperatures of 12–15 C above acclimation. At each increment above 12–15 C over acclimation temperature, delay in transit increased; however, complete group inhibition was never achieved. Above their critical thermal maximum (CTM) the reward was achieved even at the expense of deaths among the achievers. Responses were the same whether fish were challenged individually or as groups. Fish exposed to their CTM without prior challenges at less stressful temperatures responded similarly to those receiving progressively greater challenges.

The objective of this study was to determine if a laboratory test procedure would provide useful data in predicting thermal barriers to highly motivated fish movements. Many fishes make movements of varying distances to achieve dispersal of individuals and (or) to reach feeding and spawning grounds (Warren 1971). Introductions of thermal discharges across routes of transit may have adverse influences on these vital movements. Major and Mighell (1967) and Monan et al. (1975) observed thermal barriers to spawning migrations of sockeye salmon (*Oncorhynchus nerka*) and migratory rainbow trout (*Salmo gairdneri*), whose entries into spawning streams tributary to the Columbia River were halted by unusually elevated tributary temperatures. The migrants remained in the cooler Columbia River until tributary temperatures cooled. The extended time in the Columbia River before the fish could reach the spawning grounds may have been sufficient to interfere with subsequent spawning success. However, large thermal discharges to the Columbia River in the same region did not halt migrations where a zone of passage at lower temperatures was available (Environmental Protection Agency 1971; Becker 1973). In a more recent laboratory study, Gray et al. (1977) found downstream migrating juvenile chinook salmon (*Oncorhynchus tshawytscha*) only avoided water 11 C or more above ambient (acclimation) temperature.

When fish are exposed, without choice, to water temperatures above their critical thermal maximum (CTM) a fish kill results. (The CTM is defined as that temperature at which the locomotion of a fish becomes disorganized; the fish loses its ability to escape the source of distress and death will soon follow if relief is not attained: Mihursky and Kennedy 1967.) However, for cases in which fish have an option between being exposed to their CTM or remaining at more acceptable temperatures, it has not been expected that a fish kill will result, particularly when attainment of a goal by fish is highly motivated and requires that fish pass through a water mass at acutely lethal temperatures.

To gain information to aid in estimating what might be the disposition of fish encountering such a set of circumstances, laboratory tests were performed in which thermal challenges were introduced across the route of transit of juvenile rainbow trout. For greater realism, a motivating element, food, was introduced into these avoidance behavior tests. The results appear somewhat unexpected in light of reported field observations; however, the results are reasonable and may be more indicative than conventional tests of expected results under natu-

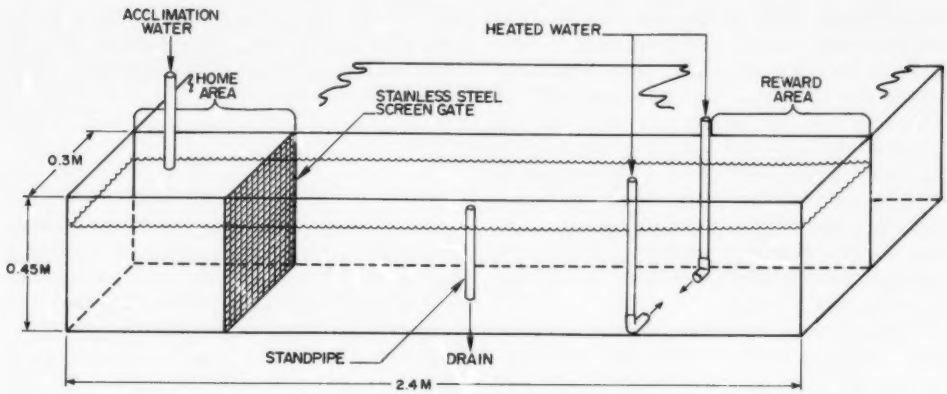

FIGURE 1.—*Physical layout of experimental channels (only one of the two duplicate channels is shown in detail).*

ral conditions where fish movements are usually purposeful.

Methods

The test apparatus was a stainless steel trough 0.6 m wide × 2.4 m long and 0.45 m deep (Fig. 1). A plywood wall running the length of this trough divided it into two equal channels each 0.3 m wide × 2.4 m long. Each channel was drained near the center by a standpipe. Water was supplied through a headbox where test temperatures were achieved by mixing waters of different temperatures via a thermoregulator-controlled solenoid valve system. Two headboxes were used: one delivered water at acclimation temperature to the home area, and the other delivered water of the desired challenge temperature to the reward area. The headboxes controlled the water temperatures to within 0.5 C of the reported means. All water entering the trough passed over aeration screens to eliminate gas supersaturation. Removable screen gates enclosed the home areas in which the fish were held between training or test trials.

In order to describe the geometry of the thermal conditions encountered by the challenged fish, representative temperature readings were taken at various intervals along each side of the trough and in the center at three depths: 2.5 cm below the surface; mid-depth; and 2.5 cm above the bottom. Examples of such data are presented in Fig. 2. The fish penetrating the heated water of the reward area had to pass through at least 0.6 m of water within 3 C of the maximum challenge temperature.

The rainbow trout was selected as the test species because migration is a well established characteristic within the species. The test fish were acquired from a local fish hatchery, and were 5–8 cm long and weighed 8–26 g. Fish not

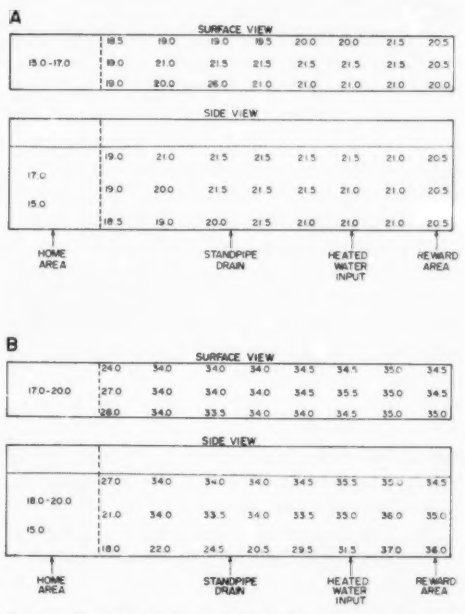

FIGURE 2.—*Temperature distribution in an experimental channel during experiments at (A) 6 C above 15 C acclimation and (B) 21 C above 15 C acclimation.*

immediately used in testing were held in another room under a 16-hour light, 8-hour dark photoperiod and were fed a meat-meal-gelatin diet (Peterson and Robinson 1967) on a feeding schedule similar to that of the fish under study. This diet was selected because it was readily accepted by the fish and because its form allowed it to be suspended in the water for a prolonged time before dropping to the bottom. The extended settling time gave the fish more time to "cue" on the food during conditioning and test trials.

Primary tests were made with a group of 20 fish in each test channel. After their introduction to the apparatus, the fish were given 24 hours to become accustomed to their new environment. Then they were confined in their home area and released only twice daily to receive food. The food was presented progressively further down the trough during conditioning until the fish traveled the full length of the trough to the reward. This conditioning procedure continued until 80% of the group traversed the trough to the reward within 2 minutes of the opening of the home-area gate. When this criterion was met, the tests began. Feeding from this time on was to repletion, but only two times per day.

Six groups of 20 fish each were tested, two groups at each of three acclimation temperatures: 6, 10, and 15 C. Test trials took place twice daily, at about 0800 and 1600 hours. Each group was released for 5 minutes and had the option of going to the reward area to feed or of remaining in the home area or at some intermediate transit location. During trials the fish were observed by the investigator from a concealed position. Behavior and counts of fish in the reward area were noted alternately at 10-second intervals. Trials were conducted at acclimation temperatures and at successive 3 C increments above acclimation until a challenge temperature resulting in deaths within the test group was reached. At the end of a 5-minute trial all fish were returned to their home area and again confined. The fish in each replicate channel were tested separately.

Two supplemental investigations employed the same appartus, the same general conditioning techniques, acclimation to 15 C, and fish from the same stock as used in the primary studies. One supplemental study used a group of 20 trained but untested fish challenged only once at the CTM determined in the primary studies. The other used two fish tested individually, each challenged at 3 C increments as in the primary studies.

Results

General Responses

Fish allowed to swim at will in the tank before testing showed no preference for or avoidance of any area. However, they were attracted to food when it was introduced into the tank. All primary trials began with the 20 fish apparently randomly distributed in their home area, some stationary and others milling about. As the screen enclosure-gate was about to be opened, the fish congregated at the gate. When the gate was opened, the fish moved, often as a group, towards the reward area. Movement to the reward area after conditioning was generally uninterrupted and followed a relatively straight course. On reaching the food, the fish fed and then moved about in or near the reward end of the channel. At challenge temperatures in excess of the CTM, deaths consistently occurred among test fish entering and remaining in the heated reward area. Fish in the peak temperature zone moved about in agitated darting motions and then, somewhat suddenly, some would make more extended and seemingly undirected dashes of 10–30 cm. This stage was followed by loss of equilibrium and death within a few minutes. If, during their random dashes, individuals happened to enter cooler waters and remained there, they would often recover with no apparent aftereffects. However, exposed fish showed no coordinated movements toward cooler water and generally did not remain in such water if they encountered it; if by random movements they failed to escape lethal temperatures death ensued.

During the trials it was impossible to follow continually the movements of each individual among the 20 fish in a test group, thus it is impossible to state that all individuals of each group made the transit to the reward at each challenge. However, since the criterion for conditioning was that 80% of the test group should achieve the food reward area in 2 minutes or less and since mortalities at challenge temperatures above the CTM are significant, it is obvious that transit to the reward among the test fish was consistently achieved, but by what per-

centage of the group can only be speculated. At least those killed can be assumed to have made the complete transit, and that a major portion of the group did so is probable. The responses of the test fish to various degrees of thermal challenge are generalized in the diagrams of Fig. 3

Responses Among Different Test Groups

Observed behavioral differences between fish acclimated to 6, 10, and 15 C were small and mostly a matter of degree. Time of transit was not as rapid at 6 C as at 15 C, and the degree of agitation when the challenge was encountered was also less at the lower temperature than at the upper. Changes in behavior among groups due to thermal challenge occurred at different absolute temperatures, but at nearly the same elevation above acclimation. Conditioning to the test-initiation criterion took fewer training trials as acclimation temperatures increased. At two training trials per day, fish acclimated to 6 C took 21 days to reach the criterion, at 10 C approximately 18 days were required, and at 15 C only 14 days were needed. Time and directness of transit to the reward area were also more concise as acclimation temperatures increased. Group training to the conditioning criterion at 15 C required about one-half as many training sessions as did training of the individuals at the same temperature.

Hesitation to move into the challenge area was first noticed at 12 C above acclimation (that is, at 27 C) among fish acclimated to 15 C, whereas among fish acclimated to 10 and 6 C such hesitation was not observed until 15 C above acclimation (25 and 21 C, respectively). Changes in the established behavior pattern, such as hesitation in movements to the food and dashes into and out of the reward area before the food was consumed, usually originated in the central portion of the trough. When challenge temperatures exceeded the CTM of the test group, 21 C above acclimation (36 and 31 C) for fish that were acclimated to 15 and 10 C, and 24 C above acclimation (30 C) for fish acclimated to 6 C, reluctance to enter the heated reward area intensified, and the first deaths among achievers resulted. However, complete inhibition was never achieved despite such deaths. Deaths reached 50% and 65% of the test groups acclimated to 15 C, 10% and 15% of the groups acclimated to 10 C, and 20% and 30% of the groups acclimated to 6 C. Once the CTM temperature was reached, as exhibited by deaths within the test groups, testing with that group was terminated. Fish challenged as a group only once (at the CTM), and individuals challenged incrementally, responded essentially the same as did the primary study groups. The group challenged only at 21 C above acclimation showed the same type of hesitation on approaching the reward area as was observed in the primary study groups, and also entered the reward area with similar lethal consequences. Within 2–2.5 minutes, all fish of this group exhibited signs of distress, rapid opercular movements, and loss of equilibrium. Eventually, 15% were inverted at the surface. On being returned to the home area, however, all recovered with no apparent aftereffects.

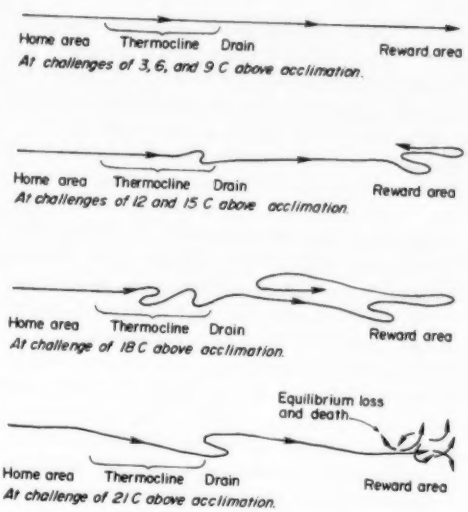

FIGURE 3.—*Diagrams of behavior patterns of test fish in response to thermal challenges between home and reward areas (fish acclimated to 15 C).*

Discussion

The conditioning criterion was reached most rapidly among those groups of fish trained at 15 C acclimation, the warmest acclimation temperature used and also that closest to a reported optimum for this species, 13.6 C (Ferguson 1958). Contributing to more rapid learning could be a greater hunger incentive at higher metabolic rates resulting from warmer temperatures and also the possible facilitation of learn-

ing at more physiologically optimal temperatures (Brett 1956; Prosser 1967; Prosser and Nagai 1968). Learning was also influenced by training-group size. Groups conditioned to the criterion in fewer training trials than did individuals at the same acclimation temperature, a phenomenon similar to that observed by Gleason et al. (1977) when studying zebra fish, *Brachydanio rerio*. Omission of the successive 3 C increases did not noticeably alter the responses of the fish to temperatures above their CTM; fish still entered high temperatures to obtain food and died as a consequence. Previous studies without such strong inducements as were employed in our study have revealed entry of fish beyond their CTM, but not in a consistent manner (Neill and Magnuson 1974). The fish in our laboratory studies did not show a clear-cut avoidance of the heated areas as would be expected from previous field and laboratory observations (Major and Mighell 1967; Monan et al. 1975; Gray et al. 1977). Hesitation in transit to the reward did not occur at the same temperature for each group, but rather it occurred at approximately the same increase above acclimation. This result also is consistent with laboratory avoidance studies showing avoidance temperatures dependent on acclimation of the test fish (Meldrim and Gift 1971; Barans and Tubb 1973). However, behavior alterations were noted at 12 and 15 C above acclimation, temperatures not unlike the 11 C change in temperature reported by Gray et al. (1977) to cause avoidance in juvenile chinook salmon without the food motivation utilized in our studies. Hesitation and back-and-forth darting as fish approached and entered heated water suggest conflicts of tendencies between the desires to feed and to avoid unendurably high temperatures. It is conceivable that apparent thermal barriers in the field occur where more than one source of urge satisfaction is available (for example, food may be obtained elsewhere), or where fish exposed beyond their CTM are carried downstream by the current to recover in the cooler mainstream waters.

Why the same thermal barriers were not found in our studies as have been previously reported under some field situations is not known. The simplest explanation may be that the motivation created by our conditioning routine exceeds that of fish who are stopped by temperatures in excess of their CTM. Nevertheless, motivation of movements in natural populations of fishes is an unavoidable factor and its influence must be considered in any testing to estimate the influence of deterrents to such movements. Our choice of food as a stimulus seems at least an adequate incentive for preliminary evaluations of the motivational factor as it might influence the magnitude of sufficient challenge to prevent normal movements.

Our data show an apparent conflict in tendencies and hesitation in transit when the fish were challenged at temperatures of 12 to 15 C above acclimation. If these responses represent those induced by thermal barriers in the natural environment, the type of test procedures reported here may be useful in predicting barrier temperatures in the field. This may be particularly true if the laboratory studies are conducted with fish acclimated at or near their ultimate upper thermal limit, since the temperatures at which movements of fishes are halted in the field may be ultimate upper thermal barrier temperatures. We believe this is probable since the fish involved may become acclimated to progressively warmer waters as they probe further into heated water seeking to achieve their goal until further heat exposure has no additional effect on acclimation and thus on avoidance temperature.

The findings of this work justify a concern for highly motivated migrant rainbow trout when heated water is introduced athwart their ancestral migratory routes. Our concern is aroused because we could not confirm the traditionally expected avoidance of temperatures above the CTM of rainbow trout when the motivation factor was introduced.

Acknowledgments

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